REVISION AND CLADISTICS OF THE MIDDLE AMERICAN GENUS *CREAGROPHORUS* MATTHEWS (COLEOPTERA: LEIODIDAE)

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Creagrophorus *is a compact genus of four Middle American species whose members eat fruiting bodies of puffballs (Gasteromycetes);* Creagrophorus hamatus *Matthews (Mexico, Panama),* Creagrophorus bihamatus *Matthews (Panama),* Creagrophorous jamaicensis *Peck (Jamaica), and* Creagrophorus spinaculeus *new species (Panama). A cladistic analysis led to the following conclusions:* Creagrophorus *is supported as a monophyletic group by apotypic broad labial palpus segment III with taeniaform seta, spines and flagellum of endophallus, absence of epicranial lines, and fimbriae of galeae and presence of four setae on segment I of the urogomphus of the larvae, transverse coxites and flattened, sclerotized styli of female genitalia, male femoral hooks (denticles), expanded middle tibia, and puffball ecological relationships; the* Aglyptinus *association is a monophyletic lineage consisting of* Creagrophorus, Aglyptinus, *and Scotocryptini, and defined synapotypically by 3-3-3 tarsi and oblique lines on abdominal sternum III;* Aglyptinus *is the sister group of* Creagrophorus-*Scotocryptini; Scotocryptini is the sister group of* Creagrophorus; C. hamatus *is the sister to the* jamaicensis-bihamatus-spinaculeus *lineage, and* C. bihamatus *sister species to* C. spinaculeus. Creagrophorus *is hypothesized to be an endemic Middle American genus, which arose after its ancestor migrated from South America where the sister group differentiated in body structure and ecological relationships (Scotocryptini); the* hamatus *lineage was isolated north of the Isthmus of Tehuantepec; the* jamaicensis *lineage was isolated in nuclear Middle America (and dispersed to Jamaica); and* bihamatus/spinaculeus *became north/south vicariants due to volcanism in the Chiriqui region.* Creagrophorus *beetles are continental in differentiation pattern, and as such are implied to have wide geographic ranges and require relatively long periods of time for speciation. The* Aglyptinus *association and* Creagrophorus *are defined, species of* Creagrophorus *described, and the following presented; keys to genera of* Aglyptinus *association and species of* Creagrophorus, *habitus drawings of adult and larval beetles, illustrations of important character states and geographic distribution, designation of lectotypes for Matthews' species, and discussions about ecological, cladistic, and zoogeographic relationships.*

Creagrophorus *est un petit genre de Leiodidae d'Amérique Centrale comprenant quatre espèces qui se nourrissent de vesses-de-loup (champignons Gastéromycètes); ce sont:* C. hamatus *Matthews (Mexique et Panama),* C. bihamatus *Matthews (Panama,* C. jamaicensis *Peck (Jamaique) et* C. spinaculeus *Wheeler, une espèce nouvelle (Panama). Une analyse cladistique permet de tirer les conclusions suivantes; les* Creagrophorus *forment un taxon monophylèetique, à cause de la présence des caractères apotypiques suivants: troisième segment des palpes labiaux large et portant une soie taeniaforme, phallobase avec épines et flagelle, absence de lignes épicraniales et de fimbriae sur les galéas, présence de quatre soies sur le premier segment de l'urogomphe chez les larves, coxas transversaux et aplatis, stylets de l'armature génitale des femelles sclérifiés, fémurs des mâles portant des crochets (denticules), tibias intermédiaires élargis, et rapports écologiques avec les vesses-de-loup; le groupe* Aglytinus *constitue une lignée monophylétique et comprend les* Creagrophorus, *les* Aglyptinus *et les Scotocryptini. Ce groupe est défini par les synapomorphies suivantes: formule tarsale 3-3-3, et présence de lignes obliques sur le troisième sternite abdominal. Le genre* Aglyptinus *est monophylétique et est apparenté aux* Creagrophorus-*Scotocryptini.* C. hamatus *est apparenté à la lignée* jamaicensis-bihamatus-spinaculeus *et* C. jamaicensis *est apparenté à la lignée* bihamatus-spinaculeus. *On pose comme hypothèse que* Creagrophorus *est un genre endémique à l'Amérique Centrale et qu'il est apparu à la suite de la migration vers le nord de son ancêtre de l'Amérique du Sud, òu le groupe apparenté (Scotocryptini) s'est différencié morphologiquement et écologiquement. La lignée* hamatus *a été isolée au nord de l'isthme de Tehauntepec tandis que la lignée* jamaicensis *a été isoleée au coeur de l'Amérique Centrale (et s'est disperée jusqu'en Jamaique). Finalement,* C. bihamatus *et* C. spinaculeus *sont devenus des vicariants, le premier au nord, le second au sud, en raison de l'activité volcanique dans la région de Chiriqui. Etant donné que les* Creagrophorus *ont un patron de différenciation continental, ils devraient avoir une distribution couvrant de vastes régions géographiques et leur processus de spéciation devrait s'étendre sur une période de temps relativement longue. On définit le groupe* Aglyptinus *et les* Creagrophorus, *et on* *décrit les espèces de* Creagrophorus. *On présente aussi une clef d'identification pour chacun des genres faisant partie du groupe* Aglyptinus *et pour les espèces de* Creagrophorus, *ainsi que des illustraions de l'aspect général des larves et des adultes, des illustrations des principaux caractères et des cartes montrant la distribution géographique. On désigne des lectotypes pour les espèces décrites par Matthews, et enfin on discute des rapports écologiques, cladistiques et biogéographiques.*

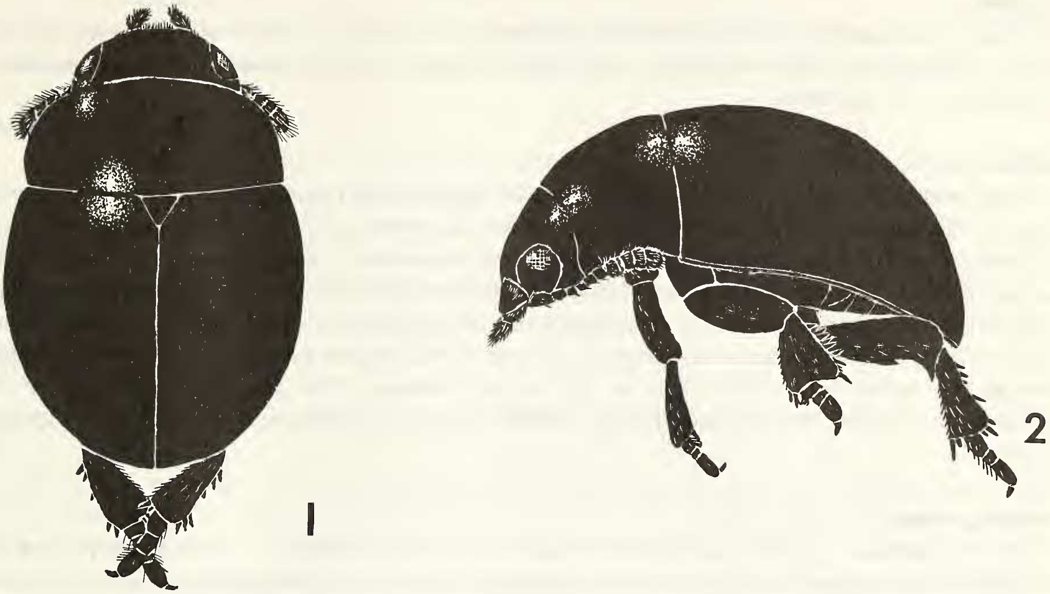
TABLE OF CONTENTS

INTRODUCTION

Small, convex, shiny beetles (Fig. 1,2) which comprise the leiodid genus *Creagrophorus* Matthews are distributed in Middle America, from central Mexico south to Panama, and in Jamaica in the Antilles (Peck, 1972). Their minute size and obscure ecological habits have made these beetles exceedingly rare in museum collections. During recent field investigations on tropical, lowland, terrestrial carabids for Terry L. Erwin (National Museum of Natural History) in Panama, I collected a large series of adults and larvae of an undescribed species and, perhaps more significantly, information about the ecological relationships of *Creagrophorus*.

Taxonomy of *Creagrophorus* has remained largely neglected since the generic description by Matthews in 1888. Peck (1977a) pointed out inconsistencies between the tarsal formula of his Jamaican species and the formula recorded by Matthews for his species. Following Peck's suggestion, I have re-examined Matthews' types and found that they, as well as Peck's species, have 3-3-3 tarsi.

Creagrophorus, together with *Aglyptinus* and the Scotocryptini apparently form a monophyletic group which I define below as the taxonomically informal *Aglyptinus* association of genera. Members of this lineage were used as the out-group for determination of character polarity in *Creagrophorus*. Lack of specimens has made decisions about cladistic and zoogeographic relationships difficult. However, sister group relationships are hypothesized using existing information about structure and ecology of *Creagrophorus* and related genera, and a few cursory observations are made about *Creagrophorus* zoogeography, based on the cladistic conclusions.



Figures 1 – 2. *Creagrophorus spinaculeus*, habitus: Fig. 1, dorsal aspect; Fig. 2, lateral aspect.

The purposes of this study are to define the genus *Creagrophorus*, revise known species, discuss ecological, cladistic (intrageneric and suprageneric), and zoogeographic relationships, and describe the larvae of a member of *Creagrophorus*.

MATERIALS AND METHODS

Materials

This study is based on about 65 adult and larval *Creagrophorus*, including type-specimens for three previously described species. Specimens of the following species were studied as out-group taxa, and voucher specimens placed in the National Museum of Natural History (USNM, listed below): *Scotocryptus* sp., *Aglyptinus laevis* (LeConte), *Aglyptinus matthewsi* Champion, *Aglyptinus* sp. (Panama), and a new species of *Aglyptinus* to be described elsewhere. The following acronyms represent collections from which material was borrowed, or into which type material is deposited:

BMNH	British Museum (Natural History), London;
CNCI	Canadian National Collection of Insects, Ottawa;
MCZC	Musem of Comparative Zoology, Cambridge;
OSUC	Ohio State University, Columbus;
QDWC	Author's private collection, Columbus;
USNM	National Museum of Natural History, Washington.

Methods

I have generally followed those methods discussed in a previous leiodid study (Wheeler, 1979), including both philosophical and procedural methods. Exceptions, modifications, and additions to those methods are discussed below.

Species criteria

I use both the theoretical and practical criteria for defining and recognizing species here as in my study of *Anisotoma* (Wheeler, 1979). Because so few specimens of *Creagrophorus* were available, delimitation of the range of intraspecific variation was impossible. I have used the structure of the aedeagus, particularly the endophallus, as a source of structures on which decisions regarding separation of species were made. Eversion of the endophallus was only possible in one species *C. spinaculeus*, since so few males were seen. Consequently, drawings of endophallus structures were prepared by observation through the median lobe. While these are only approximations of the actual detailed structure of endophallus armature, they do show distinct differences in size, number, and configuration of spines present.

Cladistic methods

My philosophical approach is essentially that of Hennig (1965,1966), as discussed previously (Wheeler, 1979). Criteria for determination of character polarity were discussed in detail by Munroe (1974) and Ekis (1977), and cladistics generally outlined by Griffiths (1972), and need not be pursued here. I have based my decisions about character polarity on out-group comparisons with taxa of the *Aglyptinus* association of genera.

Classification methods and formal ranking

My classifications of species and genera are phyletic sequence classifications as formulated and applied by Nelson (1972, 1973), Cracraft (1974), Schuh (1976), and Wheeler (1979). No formal rank is assigned to the monophyletic lineage formed by *Creagrophorus* and related genera. Rather, the informal *Aglyptinus* association of genera is proposed and defined. This allows present statements about cladistic relationships, and avoids premature reranking of Leiodini taxa before global studies are made, as suggested by Erwin (1975) as a general taxonomic rule. Similarly, I refrain from reranking the Scotocryptini now, but do state my views as to their phylogenetic significance.

Examination of larvae

Larvae were collected and stored in 70% ethanol until studied. For examination, they were cleared in Nesbitt's solution at room temperature and mounted directly into Hoyer's medium (Krantz, 1978). Magnifications up to X450 were used for observation and drawing.

Disarticulation

In addition to use of standardized dissecting methods for male and female genitalia (Wheeler, 1979), it is important to make disarticulations of entire beetles whenever possible. Inaccurate interpretations of detailed structure (e.g. tarsomere numbers in *Creagrophorus* and *Aglyptinus*, etc.) have plagued leiodid classification, but can be avoided by use of high magnification with disarticulated specimens as comparison of structures is enhanced and many additional characters are available for cladistic analysis. After disarticulation of relaxed and partially cleared specimens, parts are further cleared in dilute KOH, rinsed in water, and stored and studied in a mixture of glycerin and glycerin jelly as applied elsewhere by Wheeler (1979) and Triplehorn and Wheeler (1979). Thus parts may be oriented for view from any angle with the use of gentle heat, yet are held firmly enough for preparation of accurate drawings. I susbscribe to the views of Watrous (In press), who discusses both practical and philosophical reasons for preparing disarticulations in relation to his work with *Lathrobium* staphylinid beetles.

Descriptive format

All of the species could not be studied in the same detail as *C. spinaculeus*. Therefore, *C. spinaculeus* is described in considerable detail (including larvae), the genus diagnosed and presumed to share characters of that species except as noted, and other species diagnosed and briefly described. Where appropriate, the following are given for each species: type data, diagnostic combination, description, geographic relationships, cladistic relationships, material examined, and illustrations. Measurements were made as discussed previously (Wheeler, 1979), and are only approximations due to varying contractability of individual specimens.

COMMENTS ON FUNCTIONAL MORPHOLOGY

Aside from my observations of adult and larval *C. spinaculeus* in Panama, nothing is known about *Creagrophorus* habits. During the present study, I have developed ideas about possible functions of some structures of adult beetles. I present these ideas as possible explanations for the structures. Certainly other explanations are not difficult to conceive, but at least my ideas may stimulate further field observations which can test them and suggest realistic alternatives.

Female genitalia (Fig. 33)

Flattened, sclerotized styli of the female genitalia contrast so sharply with the plesiotypic form (i.e., lightly sclerotized, digitiform) seen in the sister group and Leiodinae in general that some specialized function is strongly implied. I hypothesize that it is an adaptation for piercing the hardened outer wall of host puffball fruiting bodies making oviposition possible, or perhaps for cutting through tough outer walls of immature fruiting bodies before their emergence above ground (see discussion under "Legs" below). Oviposition preceding apical pore formation by the host is supported by my observations in the field, although there is no reason why older fruiting bodies could not be used at times, beetles gaining entry through the apical pore.

Legs. (Fig. 16-19, 21, 22-26)

Enlargement of tibiae, presence of spines, and compaction of tarsomeres all may indicate fossorial habits. Most puffballs develop under ground until maturity, and it is conceivable that *Creagrophorus* beetles seek them out. "Primitive" Leiodini (e.g., *Leiodes* spp.) feed on hypogeous fungi (e.g., truffels: see Arzone 1970, 1971), and *Creagrophorus*, like other leiodines, retain the antennal vesicles (Crowson, 1967; Peck, 1977b), which are presumably chemoreceptive. Subterranean activities aside, adult beetles must move within the fruiting bodies in order to emerge, and these consist internally of little more than a large mass of spores. Male femoral hooks are another matter (Fig. 11-14). I do not believe they function directly in copulatory activities (males have spatulate adhesive setae on tarsomeres), but rather in some male/male aggression or male/female courtship behavior.

Mouthparts

Distinct molar teeth are not present on adult (Fig. 8,9,28) or larval (Fig. 6,64) mandibles. Such teeth were proposed as spore-crushing devices in *Anisotoma* beetles which feed on slime mold spores (Wheeler, 1979). Crenulations (Fig. 9) of adult mandibles may be homologus with these teeth, and the molar region probably still functions in spore crushing to some extent. Setae and spines of the maxillae in adults and larvae (Fig. 29,62) probably help to rake spores into the mouth. The strangest modification of the mouthparts is the taeniaform seta of the labial palpus (Fig. 3,30), for which I do not hazard a functional explanation.

The *Aglyptinus* association of genera

Creagrophorus, *Aglyptinus*, and Scotocryptini appear to consitute a monophyletic lineage. Synapotypic character states which support this arrangement are discussed more fully under "Cladistics", but include the 3-3-3 tarsomere configuration and oblique lines of the first visible abdominal sternum (sternum III). I have not made a study of Scotocryptini genera(*Scotocryptus*, *Parabystus*, *Synaristus*, and *Scotocryptodes*), and I am therefore not in a position to resolve specific problems in that taxonomic group. The current classification is based on what I perceive as weak taxonomic characters (Portevin, 1907,1937; Hatch, 1929a), and all members of Scotocryptini need to be re-examined in detail. For the purposes of this study of *Creagrophorus*, I have made the following assumptions about Scotocryptini: first, that Scotocryptini is a monophyletic group, and second, that the single species of *Scotocryptus* which I have studied is representative of this monophyletic lineage. An inevitable conclusion, if the above taxonomic arrangement is correct, is that Scotocryptini should not be alloted tribal rank. Until a study of these beetles can be made, however, I conservatively refrain from re-ranking the Scotocryptini. Nonetheless, I am convinced that it is a phylogenetically indefensible taxonomic rank.

Table 1. Phyletic sequence classification of *Aglyptinus* association genera and *Creagrophorus* species, and geographic distributions of taxa in North America (NAM), nuclear Middle America (nMA), the Antilles (ANT), southern Middle America (sMA), and South America (SAM). Numbers beside supraspecific taxa indicate number of species in area.

Taxon	NAM	nMA	ANT	sMA	SAM	Sister Group
Aglyptinus Cockerell	1	3	5	2	9	Middle and South America
Scotocryptini (4 genera)	2	0	0	1	6	Middle America
Creagrophorus Matthews	1	0	1	3	0	South and Middle America
C. hamatus Matthews	+	–	–	+	–	nMA and sMA
C. jamaicensis Peck	–	–	+	–	–	sMA
C. bihamatus Matthews	–	–	–	+	–	sMA
C. spinaculeus Wheeler	–	–	–	+	–	sMA

KEY TO GENERA OF THE *AGLYPTINUS* ASSOCIATION

Adults

1 Tarsi 3-3-3; abdominal sternum III with oblique lines (Fig. 34), *Aglyptinus* associaton.. 2
– Tarsal formula greater than 3-3-3; sternum III without oblique lines .... (other Leiodini genera, not in key)
2 Antennal club compact; tarsi compact, tarsomeres subcylindrical 3
– Antennal club loosely articulated; tarsi very long, thin; usually associated with fungi .... *Aglyptinus* Cockerell
3 Eyes present; body glabrous; labial palpus with taeniaform seta (Fig. 30); stylus of female genitalia flattened, heavily sclerotized (Fig. 33); middle tibia wider than hind tibia .... *Creagrophorus* Matthews
– Eyes absent; body pubescent; labial palpus without taeniaform seta; stylus long, digitiform; middle tibia not wider than hind tibia .... Scotocryptini
(Includes following genera: *Scotocryptus* Girard, type species *Scotocryptus meliponae* Girard; *Parabystus* Portevin, type species *Scotocryptus inquilinus* Matthews; *Synaristus* Portevin, type species *Synaristus pilosus* Portevin; and *Scotocryptodes* Portevin, type species *Scotocryptodes germaini* Portevin. Key in Hatch, 1929a).

Genus *Creagrophorus* Matthews

Type species. – *Creagrophorus hamatus* Matthews, 1888, by subsequent designation (Hatch, 1929b).

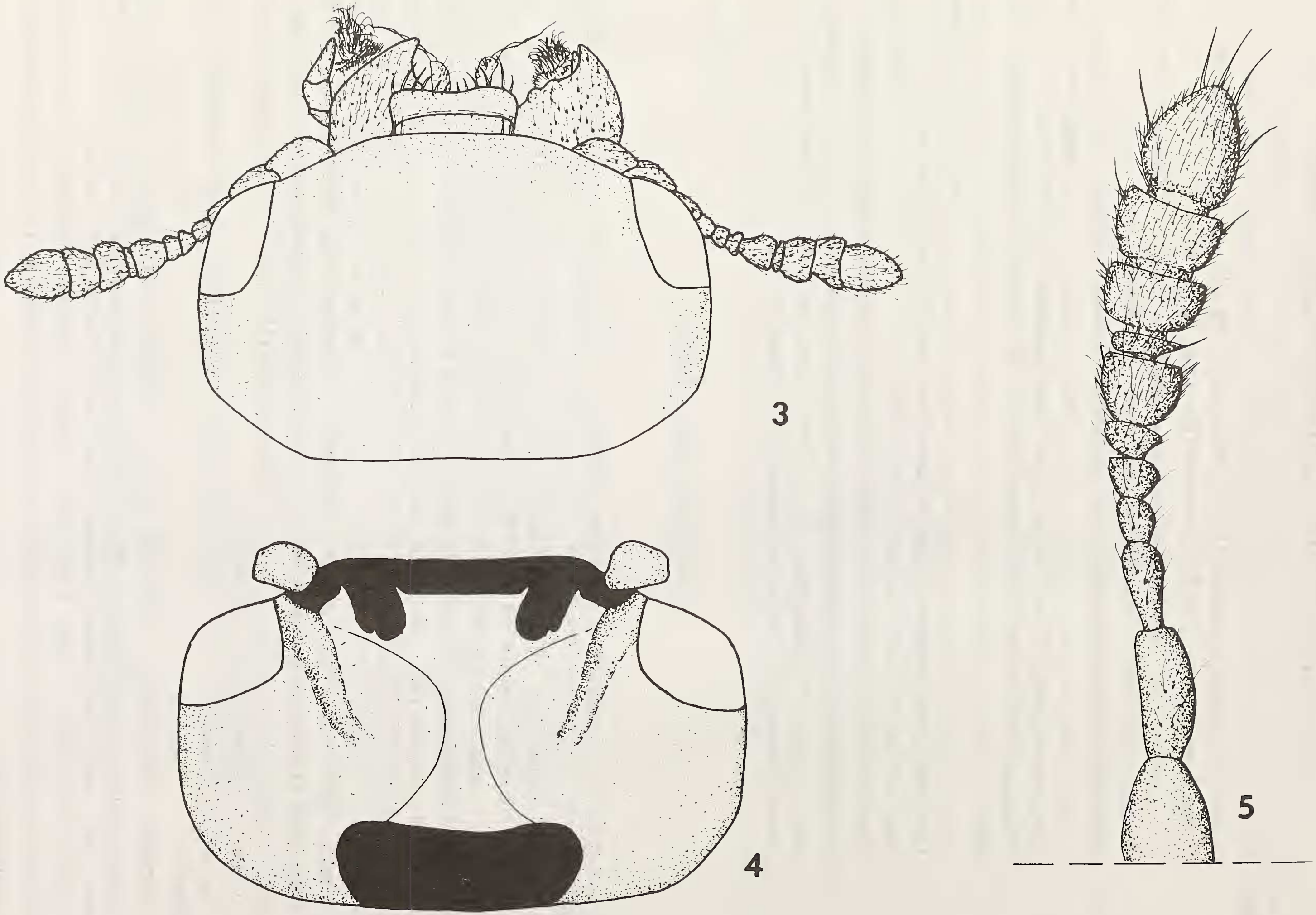
Diagnostic combination. – Staphylinoidae; Leiodidae; Leiodinae; Leiodini; ADULTS (Fig. 1,2) – Tarsi 3-3-3; abdominal sternum III with oblique lines (Fig. 34); spermathecal capsule short, broad, cylindrical, with long distal process (Fig. 35); stylus of female genitalia flattened, markedly sclerotized (Fig. 33); aedeagus ventrally curved, endophallus with large annulate flagellum and various spination (Fig. 36-40,50); middle tibia wider than hind tibia; antennal club of five antennomeres, compact (Fig. 5), antennomere VIII smaller than VII or IX; tarsi compact, subcylindrical (Fig. 24); labial palpus with taeniaform seta apically (Fig. 30); LARVAE (Fig. 53) – Galea not fimbriate (Fig. 62); epicranial lines absent (Fig. 54); urogomphal article I quadrisetose, one seta very long (Fig. 58), segment II long, crenulate; terga of abdomen each with four forked dorsal setae and one pointed lateral pair (Fig. 55); sterna with simple setae only (Fig. 56); ECOLOGICAL RELATIONSHIPS – Adults and larvae feed on fruiting bodies of puffballs (Gasteromycetes).

Cladistic relationships. – The sister group appears to be Scotocryptini, as discussed under ‘Cladistics’.

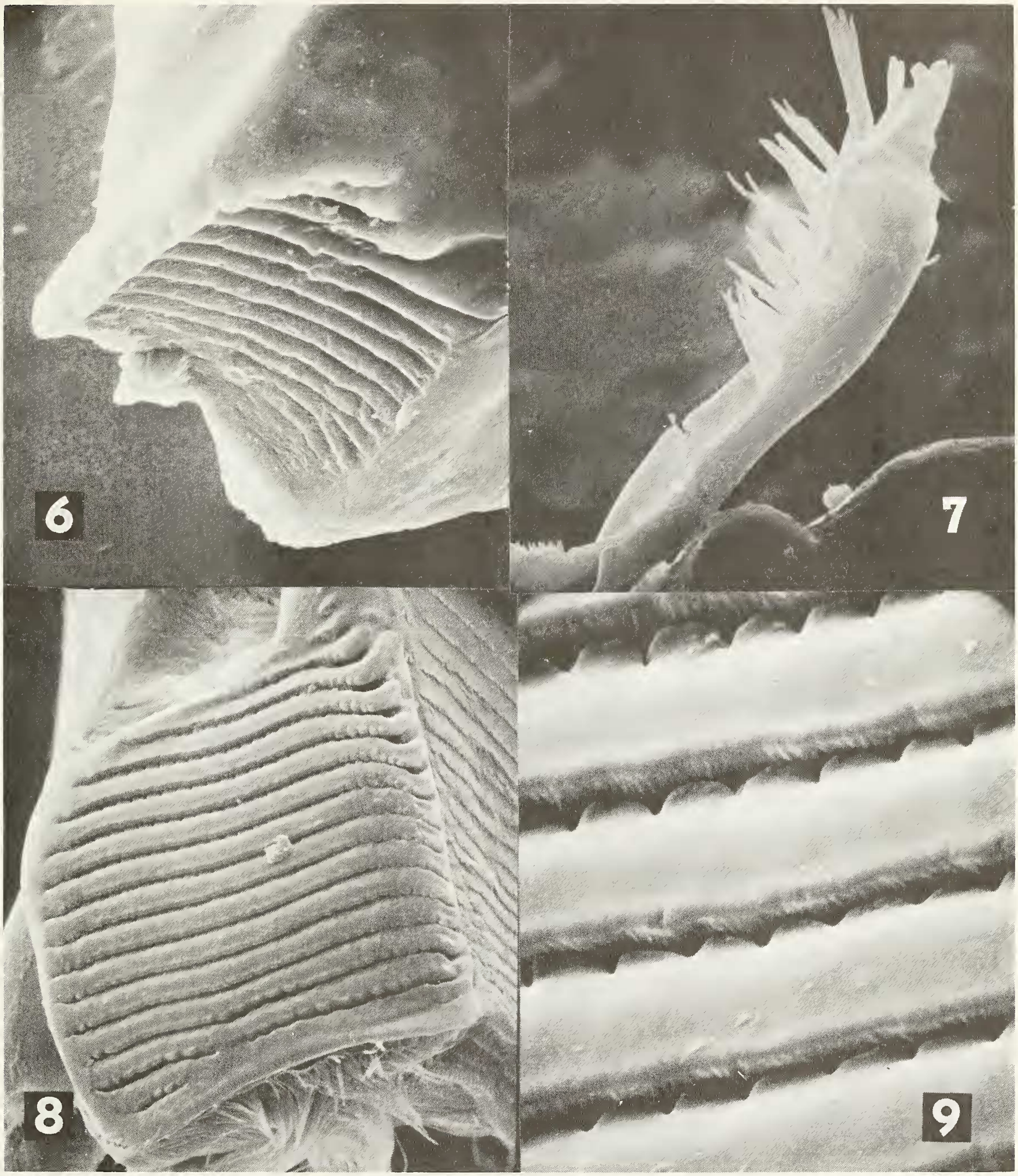
Geographic relationships. – The sister group is primarily South American with a northern subtraction pattern; *Creagrophorus* is entirely Middle American including political divisions Mexico, Panama, and Jamaica. Relationships discussed in detail under ‘Zoogeography’ section.

Species classification. – Table 1 represents a phyletic sequence classification of the species of *Creagrophorus*, and members of the *Aglyptinus* association. It is based on relationships concluded from the cladistic analysis.

Semaphoronts. – Key and descriptions of adult beetles are followed by a discussion and description of larvae.



Figures 3 – 5. *C. spinaculeus*: Fig. 3, head, dorsal aspect; Fig. 4, head, ventral aspect; Fig. 5, antenna.



Figures 6 – 9. *C. spinaculeus*: Fig. 6, mola, larval mandible; Fig. 7, prostheca, adult mandible; 8-9, mola, adult mandible.

KEY TO ADULT *CREAGROPHORUS*

1 Elytral punctures distinct; hind femur with single hook (Fig. 12); middle femur with hook (Fig. 11); endophallus with small spines near middle (Fig. 36); Mexico, Panama .... *Creagrophorus hamatus* Matthews, p. 458

– Elytral punctures indistinct or absent; hind femur with two hooks (Fig. 14); middle femur without hook (Fig. 10); endophallus with more extensive spination; Panama or Jamaica 2

2 Color black; endophallus with patches of very large spines near apex (Fig. 39,40); median lobe dorsally curved near apex (Fig. 41); Panama .... *Creagrophorus spinaculeus* new species, p. 456

– Color reddish-brown; endophallus with patches of smaller spines (Fig. 38) or small spines only (Fig. 37), lacking patches of large spines.. 3

3 Endophallus with small spines only (Fig. 37), lacking patches of large spines; female middle tiba about as wide as in male; Jamaica.........*Creagrophorus jamaicensis* Peck, p. 461

– Endophallus with two longitudinal patches of larger spines (Fig. 38); female middle tibia much narrower than in male; Panama .... *Creagrophorus bihamatus* Matthews, p. 458

Creagrophorus spinaculeus new species
(Fig. 1-10,13,15-19,22,23,27-35,39-43,69)

Holotype. – Male, USNM.

Type locality. – PANAMA, Canal Zone, Barro Colorado Island.

Paratypes. – 20, same locality as holotype; BMNH (2 males, 2 females), CNCI (2 males, 2 females), MCZC (1 male, 2 females), USNM (1 male, 7 females), QDWC (1 male).

Diagnostic combination. – Color black; shining; male hind femur bidentate (Fig. 13); female middle tibia similar to that of male; endophallus with patches of large spines near apex (Fig. 39,40).

Description. – Form subhemispherical (Fig. 1,2); length about 1 mm.

Color. Black, mouthparts, legs, and venter paler.

Microsculpture. Micropunctules distinct, moderately dense on head, increasingly sparse and obscure on pronotum and elytra.

Luster. Shining.

Head. Obovate, transverse (Fig. 3). Eyes large, conspicuous not protruding (Fig. 3). Postocular tempora not developed. Antennal grooves ventral (Fig. 4). Gular sutures subparallel at middle, divergent anteriorly and posteriorly. Antennae short, club compact, antennomeres as illustrated (Fig. 5).

Mouthparts. Labrum (Fig. 31) with six pairs apical setae, setae I-V increasing in length, VI shorter. Mandibles (Fig. 28) short, robust; apical dens large, pointed, grooved on inner margin; prostheca large, with mesal, forked cuticular processes (Fig. 7); mola with transverse grooves lined with crenulations (Fig. 8,9). Maxilla: three palpomeres, palpomere III aciculate (Fig. 29); lacinia and galea with dense tufts of fine setae. Labium: three palpomeres, III broad, curved, with several long setae medially and broad taeniaform seta apically (Fig. 30), taeniaform seta about length of palpus.

Thorax. Pronotum wider than long (Fig. 1); anterior margin medially excised; disc broadly curved. Prosternum short, medially carinate, carina forming ventrally-directed, bidentate, laminiform process. Procoxal cavities closed anteriorly and posteriorly. Mesosternum carinate; posterior intercoxal process declivous, forming transverse laminiform process. Hind wings long. Elytra broad, sutural stria complete, epipleural fold very wide basally, gradually narrowed posteriorly (Fig. 27).

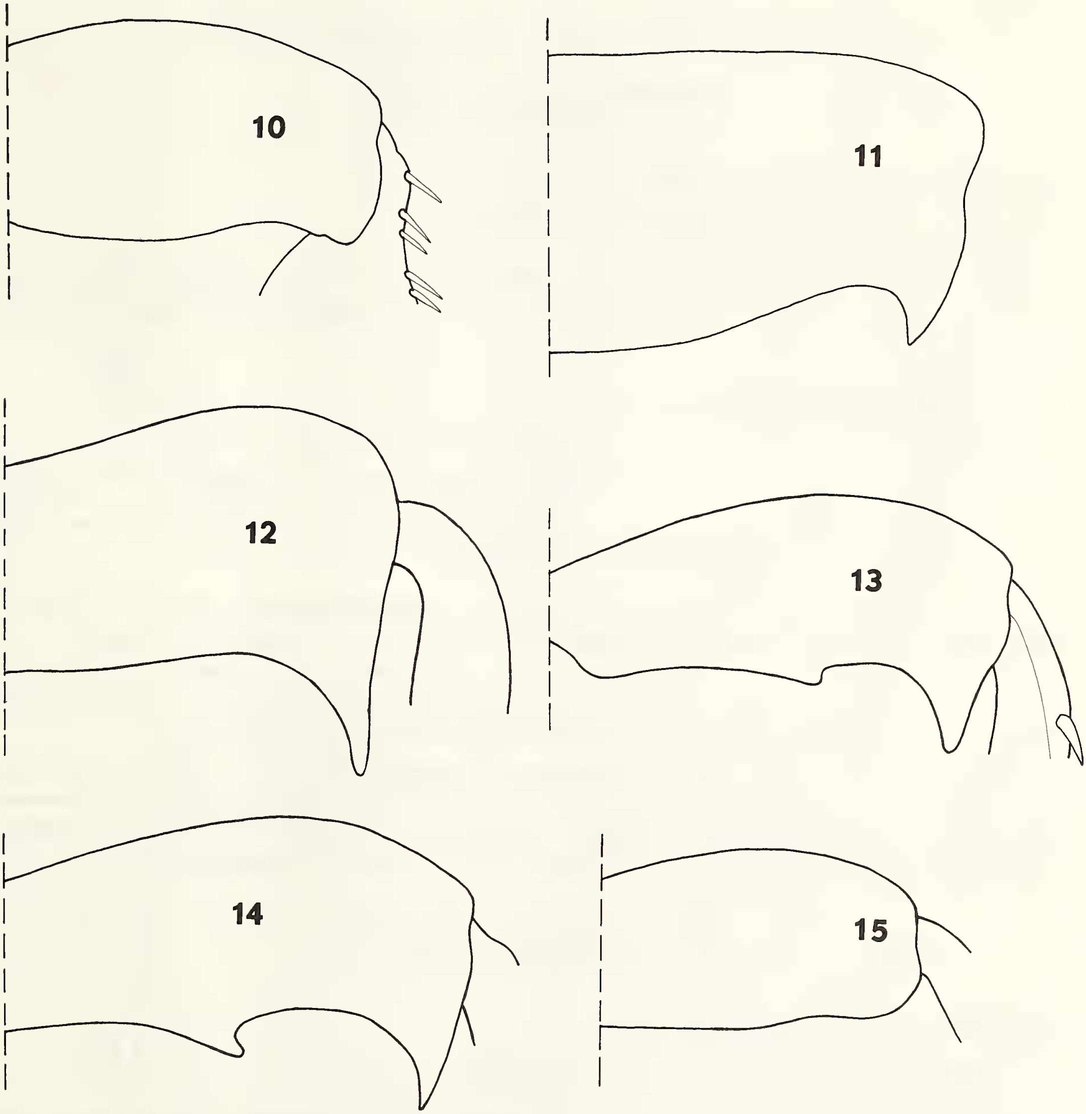
Legs. Tarsal formula 3-3-3, tarsomeres compact, subclyindrical (Fig. 17); basal tarsomere of male front and middle legs with spatulate setae (Fig. 16,18). Front tibia narrow (Fig. 16). Middle tibia greatly enlarged (Fig. 17,18,19), much wider than hind tibia (Fig. 22,23), with many stout spines. Hind tibia gradually widened. Middle femur wide. Hind femur wide (Fig. 13,15), bidentate in male (Fig. 13).

Abdomen. Sterna III-VIII visible, III-VII each with a single, transverse row of fine setae, VIII with medial and apical rows. Sternum III with oblique lines (Fig. 34).

Male genitalia. Median lobe widest subapically, narrowed at apex (Fig. 42); generally curved ventrally, apex curved dorsally (Fig. 41). Endophallus with large annulated flagellum, and apical patches of large setae (Fig. 39,40). Parameres as illustrated (Fig. 43).

Female genitalia. Coxites broad, transversely oriented. Styli lateraly curved, flattened, sclerotized, each with single stout seta and finer mesal setae (Fig. 33).

Spermatheca. Capsule short, broad, cylindrical, with tubular distal process, short tubular basal process, long, tubular, sclerotized duct leading to longer membranous duct (Fig. 35). Spermathecal gland small, membranous, inserted basally at side (Fig. 35).



Figures 10 – 15. *Creagrophorus* spp., femora: Fig. 10, *C. spinaculeus*, male, middle leg; 11, *C. hamatus*, male, middle leg; Fig. 12, *C. hamatus*, male, hind leg; Fig. 13, *C. spinaculeus*, male, hind leg; Fig. 14, *C. bihamatus*, male, hind leg; Fig. 15, *C. spinaculeus*, female, hind leg.

Geographic relationships. – This species is known only from the Canal Zone in Panama. Both *C. hamatus* and *C. bihamatus* seem to occur in Chiriqui Province, Panama. Full ranges of all three species are undetermined.

Cladistic relationships. – *C. spinaculeus* is the sister species of *C. bihamatus*, based on synapotypic occurrence of patches of large spines on the endophallus (Fig. 38,39,40).

Material examined. – In addition to specimens designated as types, one male and one female were disarticulated and are in my collection (QDWC). Illustrations were made primarily from these specimens.

Larvae. – The larvae are described under a section following descriptions of adults.

Creagrophorus hamatus Matthews
(Fig. 11,12,20,25,26,36,50-52,69)

Creagrophorus hamatus Matthews, 1888: 83.

Lectotype. – Male, BMNH, here designated (examined).

Type locality. – MEXICO, Puebla.

Diagnositc combination. – Elytral punctation distinct; male middle femur with hook (Fig. 11), hind femur with single hook (Fig. 12); reddish-brown in color; area of endophallus near middle with small spines (Fig. 36).

Description. – Length about 2.3 mm.

Color. Reddish-brown, appendages more yellowish.

Microsculpture. Sparse, fine punctules on head and pronotum, slightly larger, irregularly distributed punctules on elytra.

Luster. Shining.

Legs. Male middle tibia clavate apically (Fig. 26); middle femur with single hook (Fig. 11); hind tibia slightly clavate (Fig. 25); hind femur with single hook (Fig. 12).

Male genitalia. Median lobe ventrally curved (Fig. 50); narrowed apically (Fig. 51). Paramere fused to median lobe, in part (Fig. 52). Endophallus with small spines confined to area near middle (Fig. 36).

Female. – I have seen no females of this species.

Geographic relationships. – This is the only species of *Creagrophorus* known to occur as far north as Mexico. Matthews (1888) also records the species from Chiriqui where *C. bihamatus* also occurs.

Cladistic relationships. – *C. hamatus* is the sister of remaining species, the *jamaicensis-bihamatus-spinaculeus* lineage. The latter species share synapotypic character states including bidenticulate male hind femora, and more extensive spination of the endophallus.

Material examined. – The lectotype specimen only, labelled: SYN-TYPE (circular, ringed with blue)/TYPE (circular, ringed with red)/Puebla (hand-written), Mexico. Salle coll./hamatus (hand-wwritten)/B.C.A., Col.,II,I./Creagrophorus hamatus Matt. ♂ (hand written) det Hlisnikovsky 1961/Creagrophorus hamatus Matth., M.E.Bacchus det 197, SYNTYPE/and my labels.

Creagrophorus bihamatus Matthews
(Fig. 14,21,24,38,47-49,69)

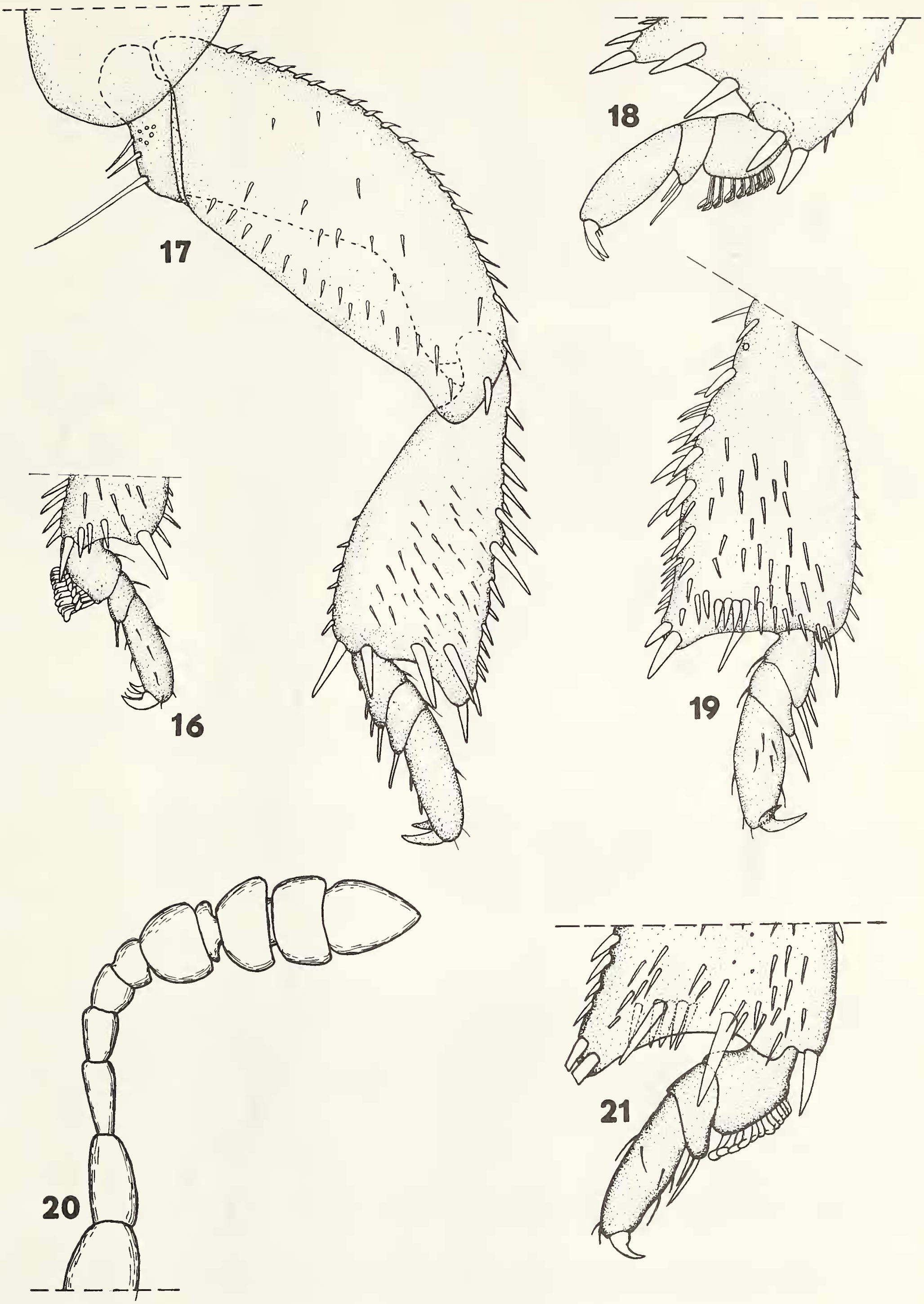
Creagrophorus bihamatus Matthews, 1888: 84.

Lectotype. – Male, BMNH, here designated (examined).

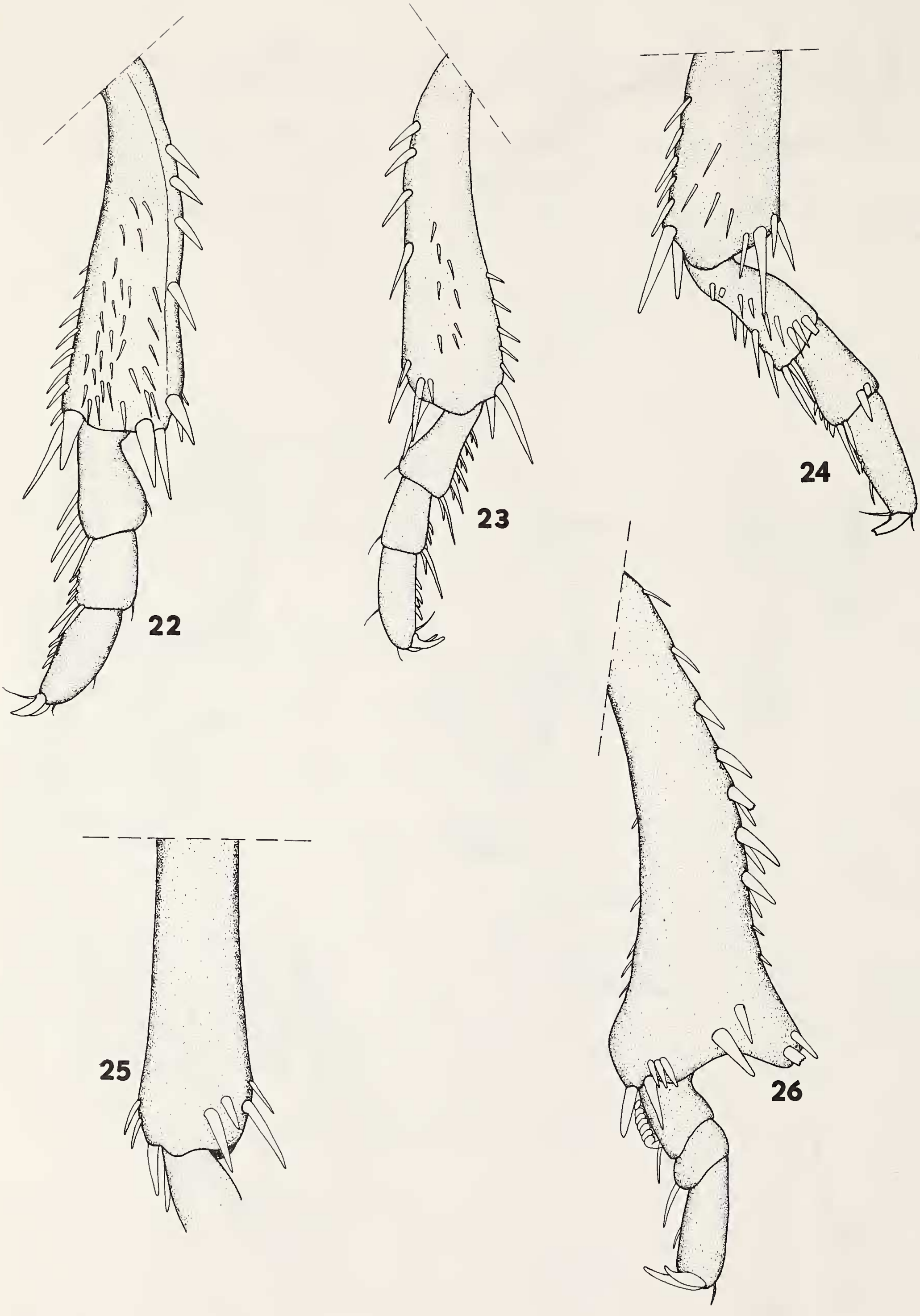
Type locality. – PANAMA, Chiriqui Province, Volcan de Chiriqui.

Diagnostic combination. – Color reddish-brown; male middle femur without hook, hind femur with two hooks (Fig. 14); endophallus with two longitudinal patches of large spines (Fig. 38).

Description. – Length about 2.1 mm.



Figures 16 – 21. *Creagrophorus* spp., legs and antenna: Fig. 16-19, *C. spinaculeus*, Fig. 16, male, front, Fig. 17, female, middle (mesal surface), Fig. 18, male, middle, Fig. 19, female, middle (outer surface); Fig. 20, *C. hamatus*, antenna; Fig. 21, *C. bihamatus*, male, middle.



Figures 22 – 26. *Creagrophorus* spp., legs: Fig. 22-23, *C. spinaculeus*, Fig. 22, male, middle, Fig. 23, female, middle; Fig. 24, *C. bihamatus*, male hind; Fig. 25-26, *C. hamatus*, male, Fig. 25, hind, Fig. 26, middle.

Color. Dark reddish brown, appendages paler.

Microsculpture. Obscure punctules on head, pronotum, and elytra.

Luster. Shining.

Legs. Male middle femur edentate, tibia broad (Fig. 21); hind femur bidentate (Fig. 14), tibia slightly wider apically (Fig. 24).

Male genitalia. Median lobe ventrally curved (Fig. 47), narrowed apically (Fig. 48). Paramere short, broad, not fused (Fig. 49). Endophallus with generally distributed small spines, and two distal, longitudinal patches of larger spines (Fig. 38).

Female. I tentatively accept the female specimen in the BMNH, identified by Matthews, as a member of this species. The middle tibia is widened only apically, the micropunctules are more distinct, and the color paler than the lectotype.

Geographic relationships. – This species occurs at Volcan de Chiriqui in Chiriqui Province, Panama. Matthews also reported *C. hamatus* from this locality.

Cladistic relationships. – *C. bihamatus* is the sister species of *C. spinaculeus*. Synapotypic occurrence of patches of large spines on the endophallus suggest this arrangement.

Material examined. – Type specimens, 1 male, 1 female, only. Lecotype male labelled: SYNTYPE (circular, ringed with blue); Bihamatus M. (hand-written); Sp. figured; V. de Chiriqui below 4,000 ft., Champion; B.C.A., Col.,II,I. In this specimen the legs on the right side are detached, on the left side they are in position (handwritten); Creagrophorus bihamatus M. ♂, det. Hlisnikovsky 1962; Creagrophorus bihamatus., M.E. Bacchus det 1978, SYNTYPE; and my lecotype labels. Female specimen (BMNH), also from Chiriqui, also figured in B.C.A.

Creagrophorus jamaicensis Peck

(Fig. 37,44-46,69)

Creagrophorus jamaicensis Peck, 1972: 56; Peck, 1977a.

Holotype. – Male, Illinois Natural History Survey, original designation (Peck, 1972) (Not examined).

Type locality. – JAMAICA, St. Andrew Parish, Hermitage Dam.

Diagnostic combination. – Color reddish-brown, luster slightly iridescent; elytral punctules indistinct; middle femur without hook; male hind femur with two hooks; endophallus with small spines, generally distributed, lacking patches of large spines (Fig. 37); Jamaican distribution.

Description. – Length about 1.2–1.4 mm.

Color. Reddish-brown, antennae paler.

Microsculpture. Punctules obscure on head, pronotum, and elytra.

Luster. Shining; somewhat iridescent.

Legs. Male middle femur without hook, hind femur with two hooks; female femora without hooks; tibiae similar in males and females, middle tibia very wide (see figs. in Peck, 1972), similar to those illustrated for *C. spinaculeus.*

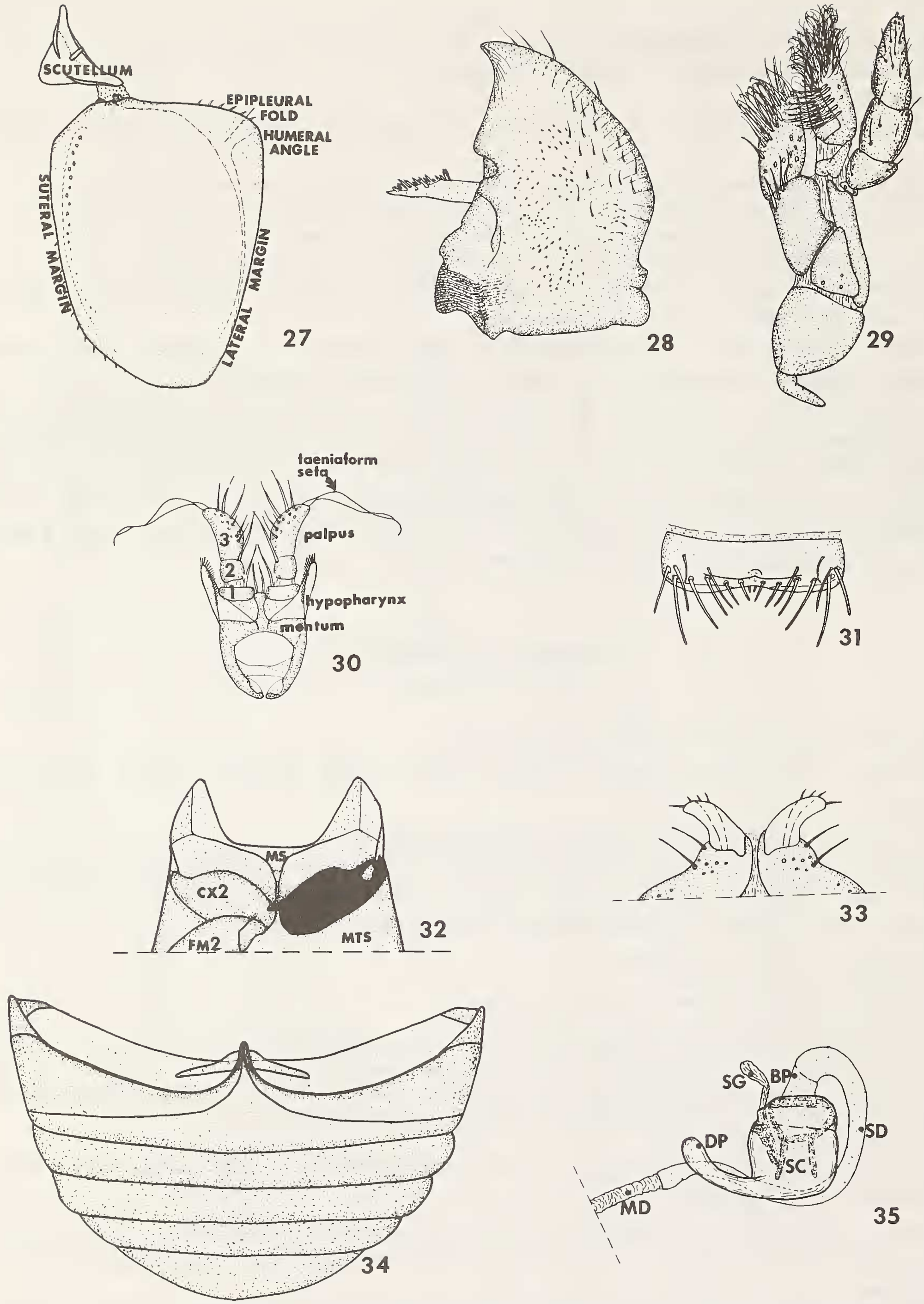
Male genitalia. Median lobe ventrally curved (Fig. 44), apex not fused, narrowed (Fig. 45). Parameres wide (Fig. 46). Endophallus with small spines, irregularly distributed (Fig. 37), without patches of large spines.

Female genitalia. Not examined.

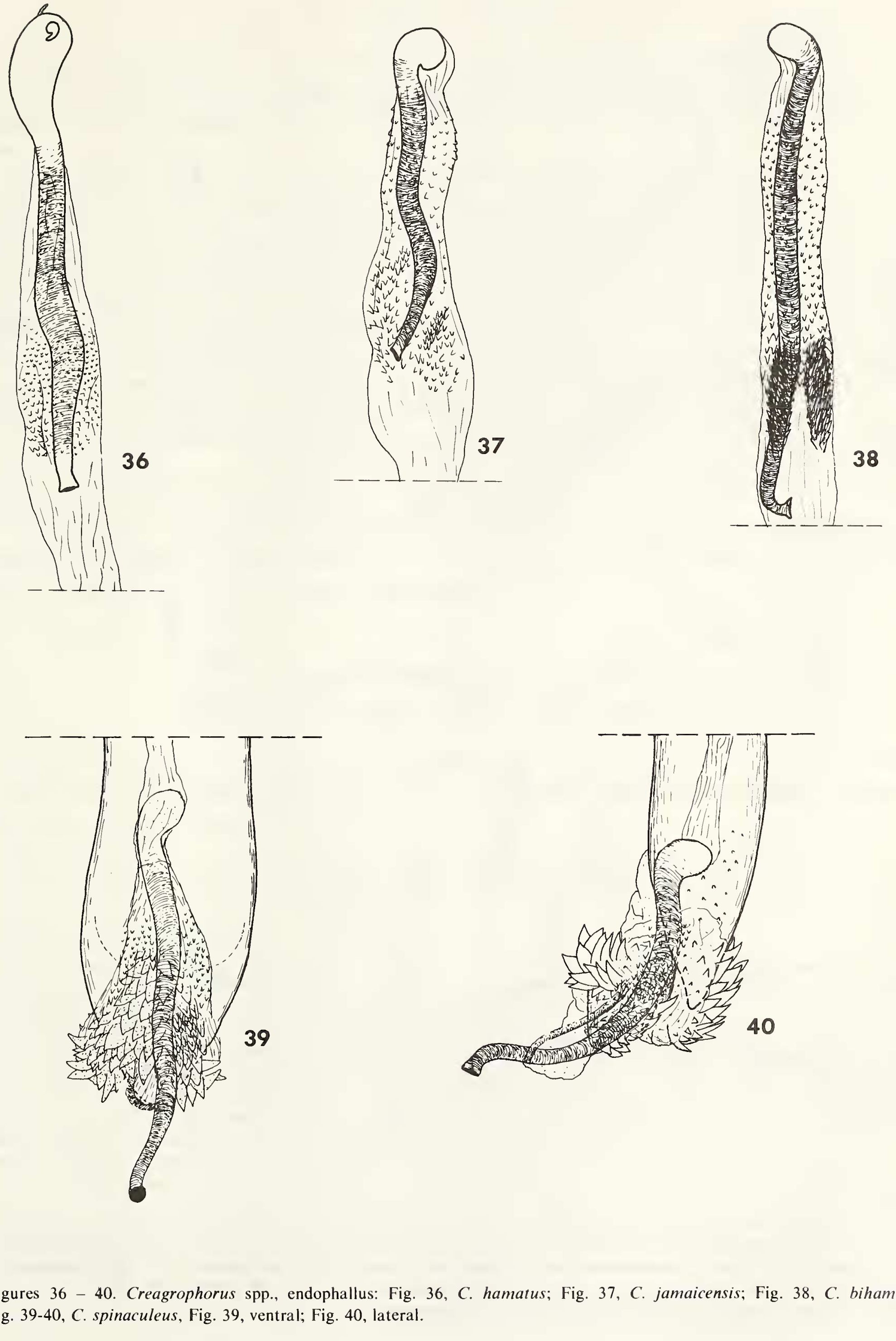
Geographic relationships. – This species is the only one which occurs in the Antilles, and is known only from Jamaica (Peck, 1972; 1977a).

Cladistic relationships. – *C. jamaicensis* is the sister taxon of the *bihamatus-spinaculeus* lineage, based on synapotypic occurrence of two hooks on male hind femur and increased spination of the endophallus.

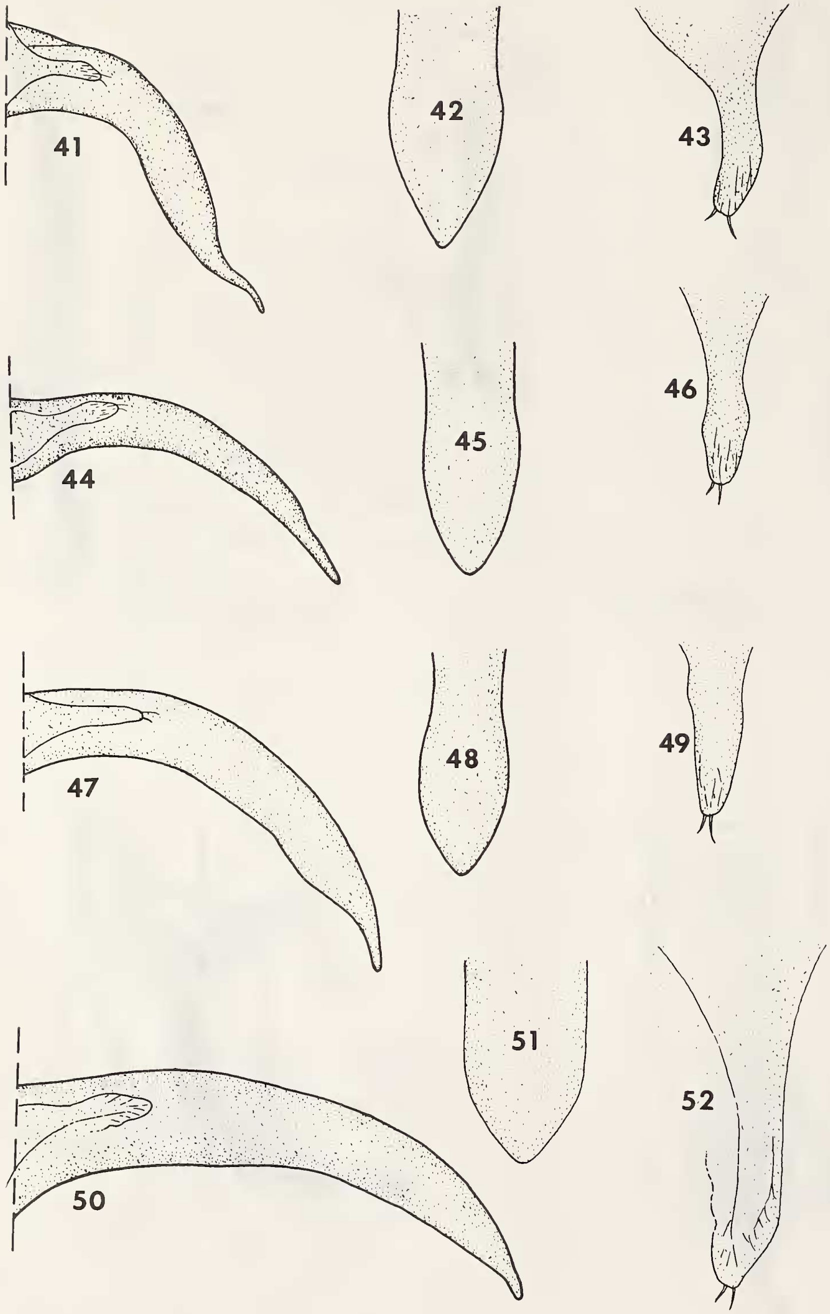
Material examined. – I have seen a female paratype (MCZC) and four specimens from Pt. Antonio, Jamaica (MCZC).



Figures 27 – 35. *C. spinaculeus*: Fig. 27, elytron, dorsal, right; Fig. 28, mandible, right; Fig. 29, maxilla, right; Fig. 30, labium, ventral; Fig. 31, labrum, dorsal; Fig. 32, meso- and meta-sterna; Fig. 33, female genitalia; Fig. 34, female abdomen, ventral; Fig. 35, spermatheca, MD (membranous duct), SD (sclerotized duct), DP (distal process), SG (spermathecal gland), BP (basal process), SC (spermathecal capsule).



Figures 36 – 40. *Creagrophorus* spp., endophallus: Fig. 36, *C. hamatus*; Fig. 37, *C. jamaicensis*; Fig. 38, *C. bihamatus*; Fig. 39-40, *C. spinaculeus*, Fig. 39, ventral; Fig. 40, lateral.



Figures 41 – 52. *Creagrophorus* spp.: Fig. 41-43, *C. spinaculeus*, Fig. 41, median lobe, lateral, Fig. 42, same, apex, ventral, Fig. 43, paramere; Fig. 44-46, *C. jamaicensis*,, Fig. 44, median lobe, lateral, Fig. 45, same, apex, ventral, Fig. 46, paramere; Fig. 47-49, *C. bihamatus*, Fig. 47, median lobe, lateral, Fig. 48, same, apex, ventral, Fig. 49, paramere; Fig. 50-52, *C. hamatus*, Fig. 50, median lobe, lateral, Fig. 51, same, apex, ventral, Fig. 52, paramere.

Larvae of *Creagrophorus*

No larvae have previously been described for *Creagrophorus*, or taxa of the *Aglyptinus* association. Information about larvae of Leiodinae has, in general, been sparse and fragmentary (Hatch, 1927; Cornell, 1972). This makes deciding which characters are of value at the genus level problematical, at best.

Leiodid beetles belong to the "Leptinid Association" of families in the Staphylinoidae (Böving & Craighead, 1931; Dybas, 1976). Dybas defined this assemblage of families with the following characters of larvae: (1) denticulate or asperate expanded molar region of mandible; (2) prostheca on inner margin of mandible; (3) urogomphi one or two segmented and articulated; (4) antennae three-segmented, with sensory appendage on segment II; and (5) galea fimbriate. Most of these characters, as pointed out by Dybas, are plesiotypic, but unite several staphylinoid families in a practical sense for purposes of discussion until phylogenetic lines become evident. Dybas (1976) gives the following combination of characters for recognition of leiodid larvae: (1) anal membrane without two prominent claws; (2) epicranial lines present; (3) ocelli present or absent; (4) compound setae often present.

Creagrophorus larvae differ from this typical pattern of characters in the following ways. The mola has distinct transverse grooves, but not distinct teeth or asperites (Fig. 6). The galea is not fimbriate. No distinct epicranial lines are apparent in any of my preparations.

It is not presently clear to me which characters will be of use at the generic level, and which at the species level. Studies of larvae in other genera will eventually make such decisions easier. Meanwhile, only *C. spinaculeus* larvae are available, and are described below.

Creagrophorus spinaculeus new species
(Fig. 6,53-64; species described above, based on adults)

Diagnostic combination. – Epicranial lines absent (Fig. 54); galea not fimbriate (Fig. 62); four pairs of forked setae on each tergum (Fig. 55) of abdomen; urogomphus segment I quadrisetose, one seta very long, segment II long, crenulate (Fig. 58).

Description. – Late-instar larva (Fig. 53), length about 2.9 mm; width across metathorax about 0.6 mm.

Form. Body subcylindrical in cross-section, widest at metathorax, gradually narrowed posteriorly (Fig. 53).

Color. White to yellowish; mandibles testaceous; more or less distinct brownish spot on each side of midline of abdominal and thoracic terga.

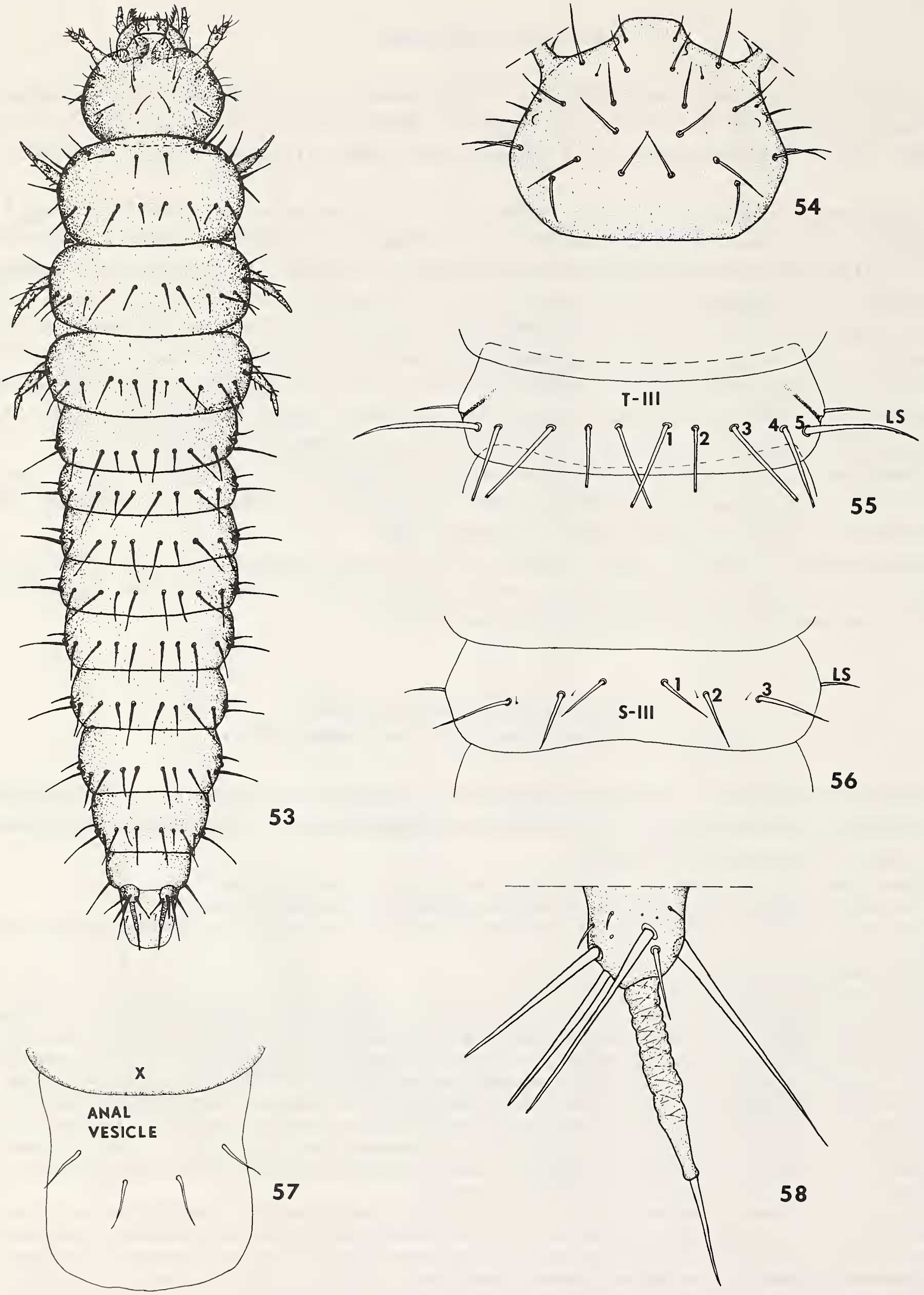
Setae. Forked or simple (pointed).

Sclerotization. Body lightly sclerotized.

Head capsule (Fig. 54). Without distinct epicranial lines. Clypeus not delimited by suture, except basolateral angles, with single pair of dorsal setae. Labrum (Fig. 60) separated by fine suture; one dorsal pair large setae medially and two pairs minute setae laterally on disc; five pairs of setae along anterior margin, medial pair small. Ocelli, two pairs. Antenna (Fig. 61) with three articles: II long, with large apical sensory appendage and smaller accessory sensory appendage; III with single stout, apical spicule. Maxilla (Fig. 62) with three palpomeres: I large, II much shorter than I, III long, thin with thin walled basal process (digitiform organ) nearly half length of III; galea not fringed (fimbriate); lacinia with comb of five stout setae, apex blade-like (Fig. 63). Labium with two palpomeres; I large, cylindrical, with apicolateral tuft; II much smaller, cylindrical, with apical tuft; ligula broad, apex rounded. Mandibles (Fig. 64) similar, except crenulations distal to median dens on right mandible, absent from left; apex pointed; molar region prominent, with many transverse ridges (Fig. 6); prostheca broad, dentiform.

Thorax. Slightly broader than abdominal segment I, terga not clearly defined. Prothorax with two transverse rows of setae: anterior row entirely of simple (pointed) setae, posterior row with four medial pairs forked setae, one pair of lateral, simple setae. Mesothorax and metathorax each with single row of setae consisting of four medial pairs of forked setae, and single pair lateral simple setae. Mesothoracic spiracle larger than abdominal spiracles, similar in form.

Abdomen. Tergum IX with single pair long, simple, posterolateral setae; all other terga with four pair forked setae, large lateral pair of simple setae, and pair of smaller, simple, post-spiracular setae (Fig. 55). Sterna with three pairs of simple setae each (Fig. 56). Spiracles small, annular, present on segments I-VIII. Urogomphus (Fig. 58) two-segmented: segment I short, wide, quadrisetose, setae simple, one very long (about length of segment II); II long, thin, gradually narrowed, basal three-fourths crenulate ("wrinkled") in



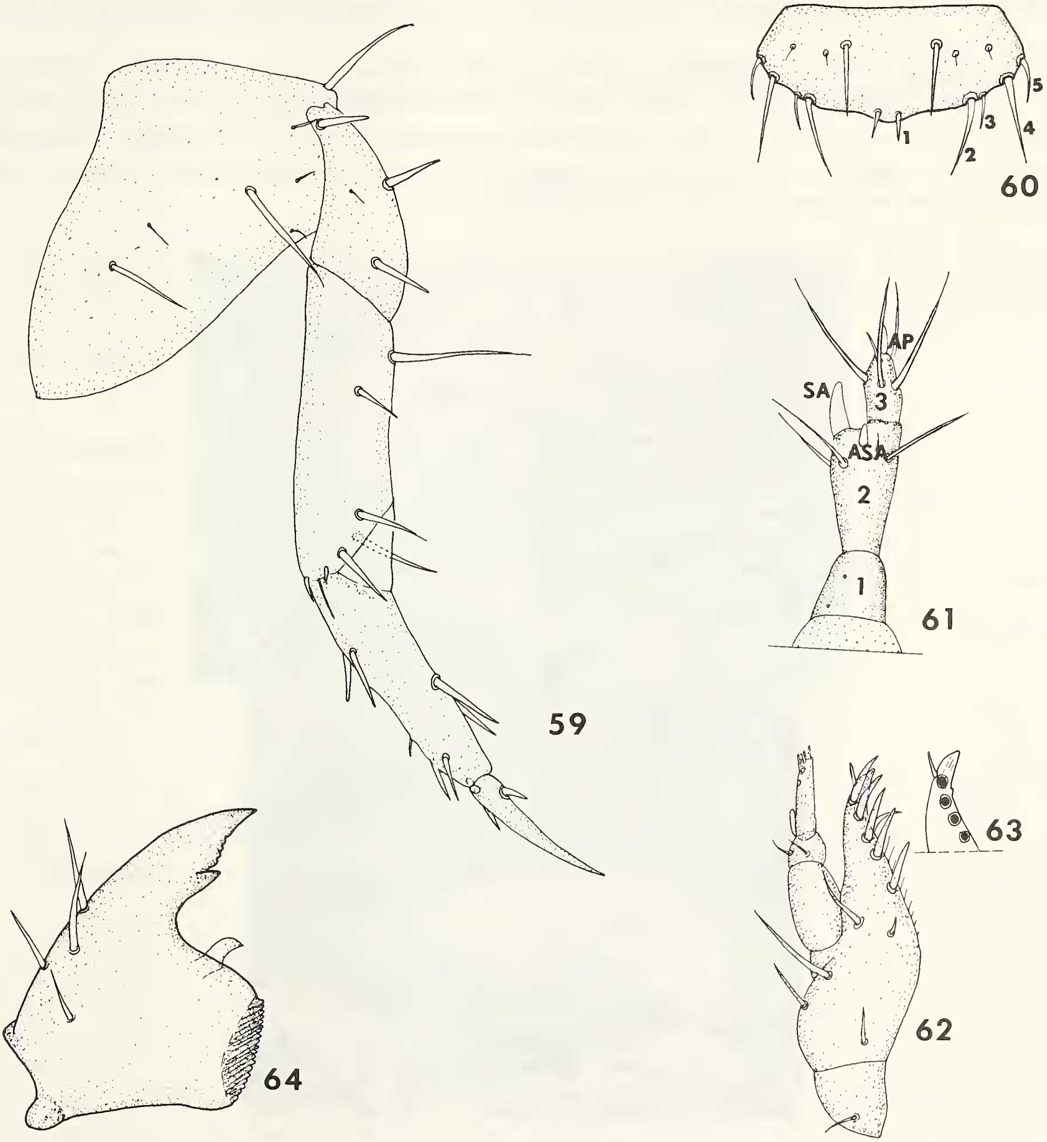
Figures 53 – 58. *C. spinaculeus*, larva: Fig. 53, habitus, dorsal aspect; Fig. 54, head, dorsal aspect; Fig. 55, abdominal tergum III; Fig. 56, abdominal sternum III; Fig. 57, anal vesicle; Fig. 58, urogomphus.

appearance with single, long, apical seta. Anal vesicle with two pairs simple setae (Fig. 57).

Legs. Similar in form to hind leg (Fig. 59).

Material examined. – About 40 larvae were collected with the type series from *Lycogalopsis solmsii* (Gasteromycetes, Lycoperdales, Lycoperdaceae) fruiting bodies in Panama, on Barro Colorado Island. About twelve larvae were deposited in the British Museum (BMNH), and remaining larvae retained in my collection (QDWC).

Comments. Larvae were observed feeding on spores inside puffball fruiting bodies in the field, and "plugs" of spores were visible in larval digestive tracts in slide preparations. No comparative statements are yet appropriate regarding relationships to other leiodids.



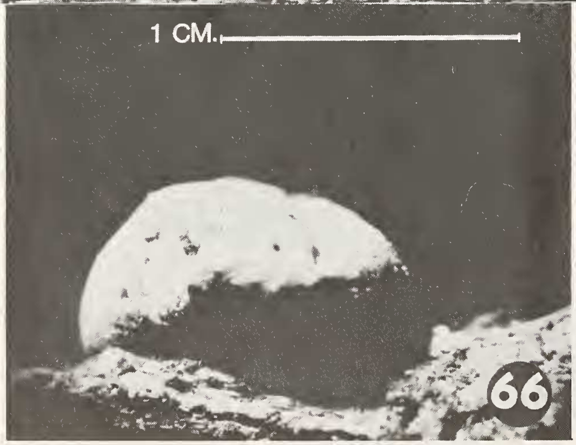
Figures 59 – 64. *C. spinaculeus*, larva: Fig. 59, hind leg; Fig. 60, labrum, dorsal aspect; Fig. 61, antenna; Fig. 62, maxilla; Fig. 63, lacinia apex; Fig. 64, mandible.

ECOLOGICAL RELATIONSHIPS

My only encounter with *Creagrophorus* was in the lowland, tropical forest of Barro Colorado Island (Fig. 65), where both adult and larval *Creagrophorus spinaculeus* were feeding in puffball fruiting bodies (Fig. 66). Although there is no way of estimating the degree of host specificity, as much information as possible about the host should be discussed as a basis for developing explanations for spatial and temporal distribution of *Creagrophorus* beetles.

The host puffball, *Lycogalopsis solmsii* Fisher (Gasteromycetes: Lycoperdales: Lycoperdaceae), is pantropical and recorded from Java (type locality), Congo, Ceylon, Japan, Puerto Rico, Martinique, and Panama. Ligneous substrata seem to be preferred, as is generally true of puffballs (Bessey, 1950; Smith, 1951; Dring, 1973).

Lycogalopsis solmsii was collected previously on Barro Colorado Island and in Balboa, both in the Canal Zone of Panama (Martin, 1939). Abundance of its fruiting bodies was recorded in Balboa during the rainy summer of 1935, but was not noticed during the drier summer of 1937. Smaller series were taken from decaying wood on Barro Colorado Island during both of those years. Moisture seems to be an important parameter for the life cycle of *Lycogalopsis*.



Figures 65 – 66. Habitat and host of *C. spinaculeus*: Fig. 65, lowland tropical forest, Barro Colorado Island; Fig. 66, fruiting body, *Lycogalopsis solmsii* (Gasteromycetes: Lycoperdales).

Larvae were found associated with the fruiting bodies in the field, and extracted by hand in the laboratory. Both larvae and large series of fully-pigmented adults fulfill the criteria established by Lawrence (1971, 1973) for recognition of valid breeding records for fungus beetles (ciids in particular).

Perhaps we can explain the absence of *Creagrophorus* from extensive leaf litter samples taken in Jamaica by Peck (1977a), if *Lycogalopsis* is fairly resricted to ligneous substrata, primarily decaying wood. It will be of great interest to collect specifically for both *Lycogalopsis* and puffballs generally to find if this is true, and what the range of acceptable hosts are for *Creagrophorus*.

Mycologists generally believe that the Gasteromycetes are closely related to (and in fact, are descendants of) the Hymenomycetes (e.g., mushrooms and related fungi). It is not difficult to imagine an *Aglyptinus*-like ancestor, already feeding on Hymenomycetes, adapting to puffball hosts.

Voucher specimens of the host fruiting bodies (*Lycogalopsis solmsii*), identified by Alexander H. Smith, have been deposited in the National Museum of Natural History (USNM) along with the type series of *C. spinaculeus*.

CLADISTICS

Cladistics are used as a method of approximate reconstruction of evolutionary pathways, as in an earlier paper (Wheeler, 1979). Character polarity determinations were based on out-group comparisons with *Aglyptinus* association taxa. Numbers in parentheses refer to characters in Table 2; references to illustrations are given in the table.

Character polarity (Table 2)

Compact structure of the antennal club (15) is interpreted as synapotypic for *Creagrophorus* and Scotocryptini. Similar compaction of clubs occurs in other Leiodini genera (ie., *Isoplastus, Apheloplastus* etc.), but I believe it is independently acquired within the *Aglyptinus* association. Eventually, intensive out-group comparisons will refine this and similar questions. The broad, flattened, curved palpomere segment III (1) of the *Creagrophorus* labium is autapotypic for the genus; *Aglyptinus* and Scotocryptini have segment III short, subcylindrical, and more or less truncate apically (the plesiotypic homologue). The taeniaform seta (2) is unique to *Creagrophorus*.

Oblique lines on abdominal sternum III (11) are synapotypic for *Creagrophorus*, *Aglyptinus*, and Scotocryptini. In general, larger body size seems typical of 'primitive' *Creagrophorus* (e.g., *C. hamatus*), and *Aglyptinus* and Scotocryptini, suggesting that smaller size (19) is apotypic for some *Creagrophorus* species. Black coloration (20) of *C. spinaculeus* contrasts with the usual reddish-brown color of *Aglyptinus* association beetles. Elytral punctation is plesiotypic in relation to the *Aglyptinus* assoctiation and Leiodini as a whole, and reduction or absence (21) is presumably apotypic. Iridescence (22) is only known in one species of *Creagrophorus* (*C. jamaicensis*). Nature of this iridescence has not been determined, but it subjectively looks different than surface gratings which occur in *Aglyptinus* sp. which will be discussed elsewhere, and is therefore interpreted as autapotypic. Hind femur hooks (8) are autapotypic for *Creagrophorus*, as are middle femur hooks for *C. hamatus* (18). 3-3-3 tarsi (12) are apparently confined to *Aglyptinus* association genera. Compact, subcylindrical tarsi (14) are shared by *Creagrophorus* and *Scotocryptus*. Expansion of the middle tibia is apotypic for *Creagrophorus*. Greater degree of expansion (29) is synapotypic in members of the *jamaicensis-bihamatus-spinaculeus* lineage.

Genital structural information is fragmentary for the out-group; that which is published is not detailed enough for evaluation here (e.g., Hlisnikovsky, 1964). I interpret available data as follows. Annulae of most of the distal portion of the flagellum of the endophallus (3) is autapotypic for

Table 2. Polarity of character states in *Creagrophorus* Matthews and related genera

No.	Character	Plesiotypic state	Apotypic state
1	Palpomere III, labial palpus	Cylindrical, truncate	Wide, flattened, curved (Fig. 30)
2	Taeniaform seta, labial palpus	Absent	Present (Fig. 30)
3	Flagellum of endophallus	Annulae absent or basal	Annulae distal (Figs. 36–40)
4	Spines of endophallus	Absent	Present
5	Article I, urogomphus	?	With four spines (Fig. 58)
6	Epicranial lines	Present	Absent (Fig. 54)
7	Galea	Fimbriate	Not fimbriate (Fig. 62)
8	Metafemoral hooks	Absent	Present (Fig. 12, 13)
9	Coxites	Long, digitiform	Short, transverse (Fig. 33)
10	Styli	Short, digitiform, lightly sclerotized	Short, wide, curved, highly sclerotized (Fig. 33)
11	Sternum III, oblique lines	Absent	Present (Fig. 34)
12	Tarsi	Formula greater than 3-3-3	Formula 3-3-3
13	Middle tibia	Slender	Expanded (Fig. 25, 26)
14	Tarsi, form	Long, thin	Compact, subcylindrical (Fig. 17)
15.	Antennal club, form	Loose	Compact (Fig. 3, 5)
16	Ecological relationship	Hymenomycete feeder (?)	Gasteromycete feeder
17	Ecological relationship	Hymenomycete feeder (?)	Meliponinae bee inquiline
18	Mesofemoral hook	Absent	Present (Fig. 11)
19	Size	Larger	Smaller
20	Color	Reddish-brown	Black
21	Punctation, elytral	Present	Absent
22	Iridescence, elytral	Absent	Present (faint)
23	Parameres	Freely articulated	Fused to median lobe, in part (Fig. 50)
24	Endophallus patches of spines	Absent (Fig. 37)	Present (Fig. 38)
25	Endophallus patches of spines	Smaller (Fig. 38)	Larger (Fig. 39, 40)
26	Median lobe	Ventrally curved (Fig. 44)	Dorsally curved over apex (Fig. 41)
27	Metafemur, male	With one hook (Fig. 12)	With 2 hooks (Fig. 13)
28	Endophallus spines	Confined to middle (Fig. 36)	More extensive (Fig. 37–40)
29	Middle tibia	Slightly expanded (Fig. 25,26)	Greatly expanded (Fig. 17)

Creagrophorus; annulae are absent from or confined to the basal portion of the flagellum in other *Aglyptinus* association taxa. Evident, broad spines of the endophallus (4) have so far only been seen in *Creagrophorus*, within which a transformational series exists. The trend is toward increased number and size of spines. *C. hamatus* is plesiotypic with only a few spines confined to middle of endophallus (Fig. 36); *C. jamaicensis* has increased numbers of spines (28); *C. bihamatus* and *C. spinaculeus* share synapotypic patches of spines (24); and spines of the patches are increased in size (25) in *C. spinaculeus*. Parameres are partially fused to the median lobe (23) in *C. hamatus*; the plesiotypic homologue is freely articulated parameres in related in-group and out-group taxa. Dorsal curvature of the median lobe (26) is unique to *C. spinaculeus* within the genus.

Transverse, short coxites (9) and flattened, short, highly sclerotized styli (10) of the female genitalia are autapotypic for *Creagrophorus*. The plesiotypic homologue for both characters involve long, lightly sclerotized, digitiform shaped structures in *Aglyptinus*, *Scotocryptus*, and Leiodinae in general.

Epicranial lines of the larval cranium seem plesiotypic in Staphylinoidea and the "Leptinid association" of families (Dybas, 1976), and have been seen in larvae identified as *Aglyptinus* and *Anistoma* (tribe Agathidiini) by me. Absence of the lines (6) from *Creagrophorus* is therefore inferred to be autapotypic. Similarly, lack of fimbriae from larval galeae (7) seems autapotypic (and was seen in the same taxa mentioned above). I suggest that the quadrisetose Article I of the urogomphus (5) may be autapotypic for *Creagrophorus* as well.

Based on observations in the field of North and Middle American species of *Aglyptinus*, I believe that the general (and plesiotypic) ecological relationship involves feeding on various fleshy hymenomycete fungi (mushrooms, etc.). Gasteromycete association in *Creagrophorus* (with *Lycogalopsis*) (16) is autapotypic, as is the inquilinism in meliponine bee nests for Scotocryptini (17).

Cladistic relationships

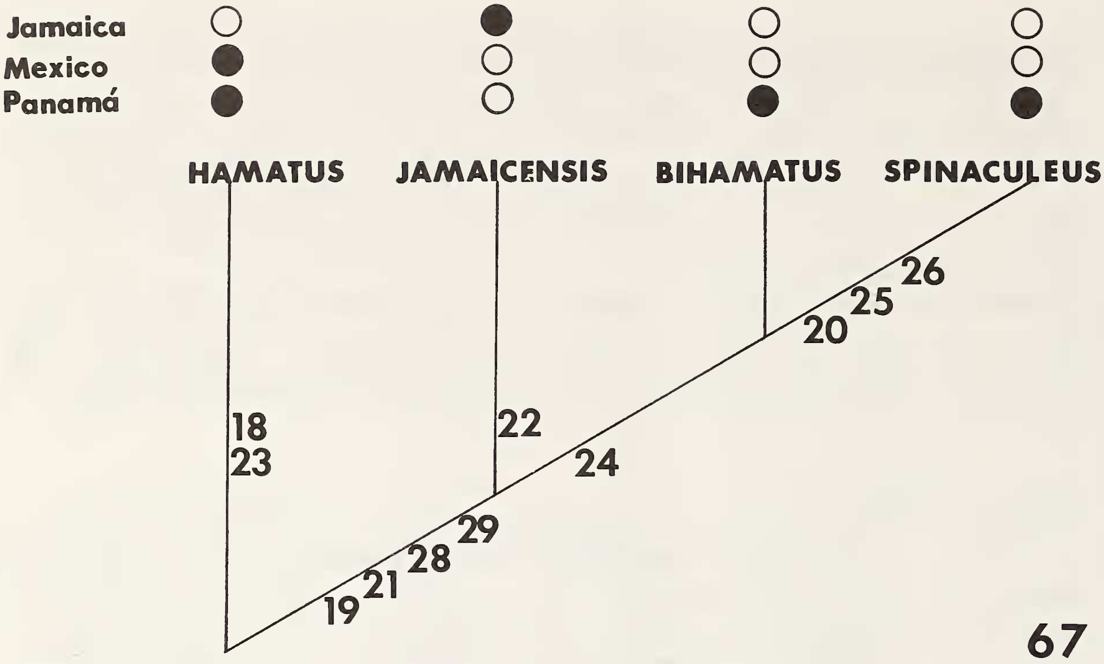
Suprageneric relationships (Fig. 68). – *Aglyptinus* association genera share synapotypic 3-3-3 tarsi (12), and oblique lines on abdominal sternum III (11). The sister group has not been identified, but will probably belong to the Leiodini *sensu stricto* (Jeannel, 1962). Compact tarsi (14) and antennal club (15) support *Creagrophorus*-Scotocryptini as a sister group pair. Their collective sister group is *Aglyptinus*, though monophyly has not been shown for that genus. Transitions to puffball feeding (16) in *Creagrophorus* and inquilinism (17) with bees in Scotocryptini are not yet understood, and a simple dichotomy subjectively seems simplistic in explaining the known extant fauna.

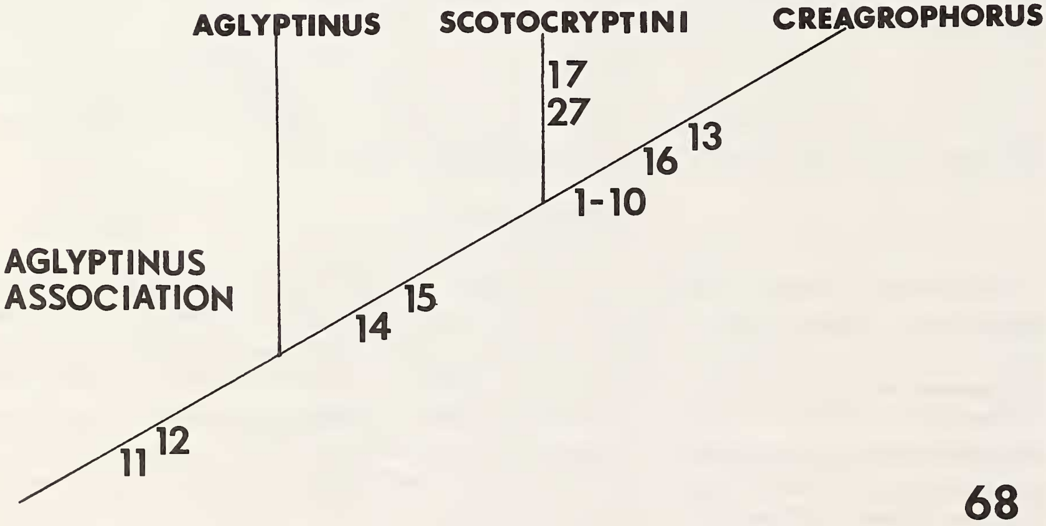
Autapotypic support for monophyletic status of *Creagrophorus* is abundant, including modifications of labial palpi (1,2), endophallus (3,4), female genitalia (9,10), legs (8,13), larvae (5,6,7) and ecologlical relationsips (16).

Intrageneric relationships (Fig. 67). – Fused parameres (23) and a hook on the middle femur of the male (18) are autapotypic for *C. hamatus*. Support for the sister lineage, *jamaicensis-bihamatus-spinaculeus*, includes increased complexity of endophallus spines (28), reduced elytral punctation (21), smaller body size (19), and greatly expanded middle tibiae (29). *C. jamaicensis* is autapotypically iridescent (22). Support for the sister lineage, *bihamatus-spinaculeus*, includes patches of large spines on the endophallus (24). Autapotypies for *C. spinaculeus* are its black coloration (20), dorsally curved median lobe (26), and large endophallus spines (25).

ZOOGEOGRAPHY

Few specimens and sparse locality information strictly limit discussions of both extant zoogeographic patterns and historical explanations for them. I concur with Whitehead (1972) and Ball (1975) who advocate provision of a theoretical basis for additional research, in the form of testable hypotheses, in every systematic study. I feel this is particularly true during early studies of a taxon, such as this one of *Creagrophorus*. General improvement in our understanding of evolutionary patterns will only come about with concern for forming and testing hypotheses, and dismissal of fears about invalidation of our ideas, as discussed by Ball (1978). It is in this spirit that I offer some interpretations of the available zoogeographic data for *Creagrophorus* and related genera.





Figures 67 – 68. Cladograms, numbers refer to Table 2: Fig. 67, intrageneric relationships of *Creagrophorus*; Fig. 68, intergeneric relationships of *Aglyptinus* association taxa.

Distribution patterns

For reasons discussed under 'Speciation patterns' below, I believe that species of *Creagrophorus* are continental in their pattern of species differentiation. I assume that species are widely distributed in suitable habitats, and that endemic populations are not common.

C. hamatus occurs in Mexico (Puebla), and was reported from Volcan de Chiriqui by Matthews (1888). I could not locate the latter specimen, but provisionally accept Matthews' identification as valid. Remaining species constitute the sister-group of *C. hamatus*. *C. jamaicensis* occurs in Jamaica, and the *bihamatus-spinaculeus* lineage in Panama. *C. bihamatus* is known only from the Volcan de Chiriqui area and *C. spinaculeus* from Barro Colorado Island, Canal Zone. Collectively, the distribution of *Creagrophorus* is Middle America, extending northward into Mexico.

Scotocryptini, sister group of *Creagrophorus* is primarily South American, with a northern subtraction pattern (Table 1). Only one species (*Parabystus inquilinus*, see Hatch, 1929b) occurring north of South America does not also have populations in South America. I suggest that this one will also represent a range extension by a South American form, or that its sister species will be South American. Scotocryptines constrast sharply with the ecological relationships of *Creagrophorus*, with their inquiline habits in Meliponinae bee nests.

Speciation patterns

Whitehead (1976) discussed criteria by which two generally distinct patterns of species differentiation may be recognized: continental and islandic. Briefly, clues for recognizing these patterns are as follows.

A. Islandic speciation pattern:
    1. High-altitude distributions, generally;
    2. Disjunct (differentiated) populations including mountaintops, caves, water-locked islands, etc.;
    3. Low-altitude distributions of organisms which are ecologically specialized or habitat-restricted.
B. Continental speciation pattern:
    1. Low-altitude distributions, generally;
    2. Continuous (undifferentiated) populations including riparian forms along streams, lowland forest forms, etc., characterized by wide geographic ranges;
    3. Ecological generalists or non-habitat-restricted organisms.

Whitehead stressed that these are only generalizations of patterns, and that every organism must be evaluated individually. Those found to conform to the islandic pattern are more likely to have been influenced by cyclic weathering of the Pleistocene than continental forms, and hence often evolve at a more rapid rate. How should the speciation pattern be interpreted in *Creagrophorus*?

At first glance, puffball feeding appears to be a rather specialized ecological relationship. Host fungi, however, are typically cosmopolitan (or in the case of *Lycogalopsis*, pantropical) within suitable climatic regions, and occur spottily over wide geographic ranges, presumably occupied by *Creagrophorus*. Fully winged adult beetles undoubtedly spend much of their time migrating from one fruiting body to another in the lowland forest, wherever microclimatic conditions permit successful growth of the host. Thus, we can assume that they have escaped major pressures from Pleistocene cyclic climatic changes, for reasons enumerated by Whitehead (1976) for lowland, tropical, terrestrial carabids, and they should be classified as demonstrating the continental speciation pattern.

Figure 69. Geographic distribution of species of *Creagrophorus*, and South American ancestral origin.

Historical zoogeography

Vicariance biogeography (see Platnick & Nelson, 1978; Rosen, 1978; Croizat *et al.*, 1974) provides a means of estimating recency of common ancestral ranges from knowledge about cladistic relationships. Congruence of a number of vicariant sister pairs may indicate a general track, which can potentially be causally explained through historical geologic events.

Constraints imposed by lack of empirical data about *Creagrophorus* geographic distribution preclude detailed vicariant hypotheses (ie., those correlating *Creagrophorus* vicariant events with those of other groups, and with known geological events). Albeit, I believe that it would be useful to discuss the general sequence of vicariant events indicated by present data. Tests and substantiation of these ideas would make more detailed biogeographic analyses possible.

Historical scenario. – Ancestral *Creagrophorus* entered Middle America from South America (Fig. 69), became widespread, and differentiated from the southern ancestral stock which is today represented by Scotocryptini. The scotocryptines have become specialized for inquilinism in Meliponinae bee nests. The first vicariant event isolated the *hamatus* lineage to the north of the Tehuantepec portal. The second was a division of nuclear Middle American and southern Middle American stocks (the nuclear stock dispersed to Jamaica). The third vicariant event isolated sister species to the north and south of the Chiriqui volcanic region (*bihamatus* to the north, *spinaculeus* to the south).

Predictions. – Any discussion about zoogeography at this early date in studies of *Creagrophorus* is meaningless without some obvious utility to later research. Therefore, I offer the following predictions as a framework for continued study.

1. Species conform to a continental pattern, enjoying wide geographic ranges.
2. If *C. hamatus* is actually widespread, no additional species of the *hamatus* lineage will be found which have originated in Middle America and/or are adapted to the same hosts.
3. The *jamaicensis* lineage is represented in nuclear Middle America by either *C. jamaicensis* itself or its sister species. If *C. jamaicensis* has mainland populations, then no additional species is predicted. Similarly, if *C. jamaicensis* is widespread in the Antilles, no other insular members of the *jamaicensis* lineage are expected.
4. *C. bihamatus* occurs throughout southern Middle America, north of Chiriqui. Absence of this a species from nuclear Middle America is a corallary of the presence of a member of the *jamaicensis* lineage there in prediction 3.
5. *C. spinaculeus* is the southern vicariant of the Chiriqui barrier. It is either allopatric or parapatric with *C. bihamatus*.
6. *C. bihamatus* and *C. spinaculeus* actually share a most recent common ancestor (ie., no additional species of the *bihamatus-spinaculeus* lineage exist).
7. The sequence of vicariant events hypothesized above require that no additional branching points exist on the lineage leading to *bihamatus-spinaculeus*. Specifically, the *jamaicensis* lineage is the sister of the *bihamatus-spinaculeus* lineage, and the *hamatus* lineage sister to these collectively.
8. *Creagrophorus* is absent from South America. If any species do exist there, they will not be part of the Middle American lineage.

Some aspects of the historical scenario and the predictions are bold extrapolations from a limited amount of empirical data. My intent is to set forth possible explanations for the observed pattern of distribution, which can subsequently be field-tested and supported or rejected. The eventual outcome should be the same: approximation of the actual sequence of events leading to present *Creagrophorus* patterns. These ideas will minimally serve as a template for arranging later observations and a stimulus to continued field work in puffball/leiodid beetle relationships.

CONCLUSIONS

Many conclusions have been reached in this study which are stated or implied within the text. It would be useful, however, to draw some conclusions of a general nature from the study as a whole. There remains much to be done in the field before ideas about ecological and zoogeographic relationships of *Creagrophorus* beetles become stable. I hope that this study has set the stage for such investigations. I urge detailed study of the Scotocryptini, and suspect that the tribal status must be abandoned, based on my cladistic analysis. My discussion of the larvae is a minor contribution to an area of study in the Leiodinae which is virtually untouched. Ecological data, though limited, should now be sufficient to allow (and stimulate) the accumulation of specimens and information about hosts and geographic distributions throughout Middle America.

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Index to Names of Taxa